Leaf Extrafloral Nectaries Enhance Biological Control of a Key Economic Pest, *Grapholita molesta* (Lepidoptera: Tortricidae), in Peach (Rosales: Rosaceae)

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ABSTRACT   Extrafloral nectaries (EFNs) in many plant species produce sugary secretions that commonly attract ants. This research determined the impact of peach (*Prunus persica* L. Batsch) EFNs on the biological control of the oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae), a key economic pest in peach orchards, and studied interactions of EFNs and ants. Studies (2002–2005) in peach orchards of the mid-Atlantic United States showed that 'Lovell' peach trees with EFNs supported more parasitic Hymenoptera in the spring and increased the parasitism of *G. molesta* larvae later in the season than those trees without EFNs. Ant exclusion experiments revealed that trees with EFNs harbored fewer *G. molesta* larvae when ants were permitted access to the tree canopies. Furthermore, the trees with EFNs had ≈90% less fruit injury by *G. molesta*, indicating that EFNs have a protective role for the fruit as well. The results show that the combined actions of ants and parasitic Hymenoptera confer an EFN-mediated protective effect spanning the whole fruit growing season. When EFNs are present, naturally occurring biological control agents can reduce damage by *G. molesta* in peach orchards without insecticide inputs. The EFNs are an important host-plant characteristic that should be retained in future peach cultivar selections as a means of enhancing biological control.

KEY WORDS   conservation biological control, *Grapholita molesta*, *Prunus persica*, Formicidae, extrafloral nectaries

The extrafloral nectar of plants is a valuable food source for adults of some ichneumon and braconid parasitoids (Stapel et al. 1997, Baggen et al. 1999) and may be important in efforts to conserve these and other natural enemies (Barbosa 1998, Bugg and Pickett 1998, Gurr et al. 1998, Landis et al. 2000). However, except for cotton (*Gossypium* sp.), the influence of extrafloral nectar on parasitoid effectiveness in crop plants is largely unknown (Beattie 1985, Rogers 1985). Plant breeders have developed new cultivars of agricultural and horticultural crops without considering the potential consequences of extrafloral nectaries (EFNs) on natural enemies.

Most peach (*Prunus persica* L. Batsch) cultivars have EFNs on the leaf petioles, stipules, or margins (Gregory 1915, Okie 1998). Peach EFN secretions include carbohydrates and amino acids (Caldwell and Gerhardt 1986) that adult parasitic Hymenoptera need for energy and egg formation (Vinson and Barbosa 1987, Lewis et al. 1998). EFN production for *Prunus* sp. is higher in young than in old leaves and peaks in early spring (Putman 1963, Yokoyama and Miller 1989). The EFN secretions could potentially sustain adult parasitoids in early spring before their insect hosts colonize the peach trees and therefore enhance biological control of pest herbivores (Hodek 1962, Price et al. 1980, Van Emden 1990, Barbosa and Benrey 1998, Landis et al. 2000). *Macrocentrus ancylivorus* (Roh.), an important parasitoid of the oriental fruit moth [*Grapholita molesta* (Busck)], lived longer on young peach leaves that produced greater amounts of extrafloral nectar than on older leaves (Putman 1963). In the laboratory, peach extrafloral nectar increased longevity of and egg parasitism by the oriental fruit moth egg parasitoid *Trichogramma minutum* (Shearer and Atanassov 2004). However, no one has determined how parasitic Hymenoptera respond to peach EFNs in the field.

Modern fruit breeding programs have inadvertently produced peach cultivars with the EFNs removed (Okie 1998) without determining the effects on either natural enemies or herbivorous pests (Scorza and Sherman 1996). Recent findings indicated that the arthropod community structure of newly planted peach orchards changed significantly when EFNs were removed (Mathews 2005). Ants were numerically dominant on trees with EFNs but were scarce on trees without EFNs (Mathews 2005). The predominance of ants on EFN-bearing trees could reduce the

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effectiveness of parasitic Hymenoptera. Ants have disrupted mealybug [*Dysmicoccus brevipes* (Cockerell)] parasitism by *Anagyrus ananatis* (Gahan) in pineapple (Gonzalez-Hernandez et al. 1999) and reduced scale [*Aonidiella aurantii* (Maskell)] parasitism by *Aphytis melinus* (DeBach) in grapefruit [*Citrus paradisi* (MacFayden)] (Murdoch et al. 1995). It is therefore important to understand the potential for competitive interactions among ants and parasitic Hymenoptera that feed on EFN secretions in peach orchards.

The research described here explored the impact of peach EFNs on biological control of the oriental fruit moth, a key economic pest of peach in the mid-Atlantic United States (Allen 1962, Hogmire 1995). *G. molesta* females deposit eggs on the underside of leaves of newly emerged shoots or directly on peach fruits, and neonate larvae feed internally in the fruits and young terminals (Rothschild and Vickers 1991). The 'Lovell' peach cultivar in these studies is heterozygous for the leaf EFN trait (Okie 1998). When selfed, 'Lovell' produces some offspring with reniform EFNs (large, kidney shaped glands producing nectar) and others that are aglandular (no EFNs or nectar produced) (Connors 1922, Okie 1998). Therefore, EFN effects can be studied while holding other host plant characteristics (e.g., canopy architecture, host plant volatiles, and fruit attributes) constant. The research specifically studied the effects of peach EFNs and ants associated with them on the relative abundance of *G. molesta* and parasitic Hymenoptera, rates of *G. molesta* parasitism, and fruit damage by the pest.

Materials and Methods

Studies were conducted between 2002 and 2005 in orchard plots of the 'Lovell' peach cultivar planted in April 2002. Plots of a peach leaf phenotype (EFNs present or EFNs absent) were established in a completely randomized design at two sites (USDA Appalachian Fruit Research Station, Kearneysville, WV, and University of Maryland Western Maryland Research and Education Center, Keedysville, MD). The field design included four replicates (each 0.25 ha, spaced 33 m apart) separated by a buffer hedgerow of hybrid willow (*Salix* sp.) trees. A replicate consisted of two orchard plots (each with 40 peach trees, planted in five rows at 5 by 3-m spacing) separated by an additional *Salix* sp. buffer hedgerow. Treatments (EFNs present, EFNs absent) were randomly assigned to plots within replicates so that all peach trees in a plot had the same leaf phenotype. To minimize disruption of arthropod interactions in the orchard plots, maintenance during the study months was limited to two selective herbicide applications, mechanical weed cultivation (three times per year), and fungicide applications (one or two per year) to control powdery mildew [*Sphaerotheca pannosa* (Wallroth ex Fr.) Lév.]. Chlorpyrifos (3.4 kg [AI]/ha) was applied to the base of each tree to control peach tree borer, *Synanthedon exitiosa* (Say), every October. No insecticides were applied during the sampling periods May to September.

In 2003, an ant exclusion method was used to measure how ants affected other natural enemies when EFNs were present and absent. The main plots (EFNs present, EFNs absent) were split into two subplots (ants present, ants absent). Eight peach trees were randomly selected from each main plot. Four of the trees received the ant exclusion treatment and the other four served as controls, resulting in a completely randomized design split-plot design (leaf EFN phenotype = whole plot factor; ant exclusion = subplot factor). To exclude ants, a 2-cm-wide strip of Tangletrap (Tanglefoot Co., Grand Rapids, MI) was applied to 5-cm-wide masking tape wrapped around a tree's trunk (≈30 cm above ground) on 3 April 2003. The trunks of the control trees were also wrapped with masking tape but without Tangletrap.

Parasitic Hymenoptera Abundance. A sticky trap positioned in a peach tree's canopy was used to estimate the relative abundance of parasitic Hymenoptera monthly during 2002 (18 June, 3 July, and 22 August) and 2003. In 2003, the interval between sticky trap samples was shortened to 2 wk (29 May, 10 and 26 June, 7 and 29 July, and 14 and 28 August). Eight randomly selected trees per plot were sampled both years (2003: four trees with ant exclusion, four trees without ant exclusion). Sampling on trees with EFNs was confined to terminals with active EF-nectar production, confirmed by visual inspection at the start of the sample period. In 2003, trees also were inspected for the presence of potential confounding factors, such as honeydew-producing homopterans (e.g., aphids). The sticky traps were clear 18-cm-diameter plastic dinner plates with their inner 15 cm diameter coated in a thin layer of Tangletrap. In each tree, a trap was suspended by string from a randomly selected terminal ≈36 cm above the lower margin of the tree canopy. After 24 h, traps were covered with saran wrap, transported to the laboratory, and frozen until the captured insects were identified. In 2002, the parasitic Hymenoptera were identified only to order. In 2003, they were identified to at least superfamily. Parasitic Hymenoptera identifications were verified by David Biddinger (Pennsylvania State University Fruit Research and Education Center, Bigglerville, PA). Parasitoid abundance data for the sample trees within a treatment plot were averaged to avoid pseudo-replication within a sample period.

Data for sample periods of each year were log transformed for statistical analysis. Separate analyses were performed for the total parasitoid collection and for the specific taxa commonly reported to attack *G. molesta* larvae (i.e., Braconidae) and eggs (*Trichogramma* sp.). For the 2002 data, an analysis of variance (ANOVA) tested for the effect of EFNs on parasitoid densities (PROC MIXED; SAS Institute 1999). For the 2003 CRD split-plot study, the ANOVA tested for main effects of EFNs and ant exclusion and also EFN-ant interactive effects (PROC MIXED; SAS Institute 1999). When ANOVA indicated a significant treatment effect, means were separated by the least-squares difference procedure using the Bonferroni adjustment to correct for multiple comparisons

(LSMEANS/ADJUST = BON, α = 0.05; SAS Institute 1999).

***Grapholita molesta* Abundance and Natural Parasitism Rates.** *Grapholita molesta* populations were monitored four times in 2002 (24 May, 23 June, 23 July, and 19 August) and 2003 (29 May, 26 June, 22 July, and 14 August). The sampling spanned the period when *G. molesta* normally infests peaches in the mid-Atlantic region (Hogmire 1995). Eight randomly selected trees per plot were sampled both years (2003: four trees with ant exclusion, four trees without ant exclusion). An entire tree was visually inspected for injury to new shoots (commonly referred to as "flagging") and frass characteristic of *G. molesta* later instars feeding in stems (Rothschild and Vickers 1991). The total number of flagged shoots and larvae (one flagged shoot = one larva) per tree was recorded. To avoid recounting injured terminals in subsequent samples, flagged shoots ($\approx$12 cm long) were cut off. Each of the shoots cut off in 2003 was held in a 710-ml paper cup (Solo Cup Co., Urbana, IL) for emerging *G. molesta* moths and adult parasitoids. A store-bought red apple (variety 'Red Delicious'), washed with dish soap to remove wax coating and rinsed with deionized water, was added to each cup as food for larvae emerging from the shoot (Bobb 1939). Cups were covered with nylon mesh and held in a growth chamber (22°C, 16:8 L:D photoperiod) and checked weekly for *G. molesta* adults and parasitoid adults. Parasitism was calculated as percentage of potential hosts (i.e., shoots from which either an adult moth or adult wasp emerged) from which an adult parasitoid emerged.

Limb jarring was conducted concurrent with *G. molesta* sampling to detect the presence of ants in the tree canopy (2003). Each of two randomly selected terminals per tree was tapped twice with a rubber hose to dislodge arthropods, and ants falling on a 0.58-m^2 collecting canvass beneath the terminal were recorded. The canvass was also inspected for honeydew-producing homopterans (e.g., aphids) that could potentially provide sugar resources for ants. Commonly appearing ant species were collected and later identified by Jeffrey Sossa (Department of Systematic Biology, Ant Laboratory, Smithsonian Institution, Washington, DC) and Sean Brady (Laboratory of Analytical Biology and Department of Entomology, Smithsonian Institution, Suitland, MD).

Graphical examinations and univariate analyses suggested that data within sample periods of a year met the assumptions of ANOVA. For 2002 data, ANOVAs (within sample periods) tested for the effect of EFNs on *G. molesta* densities (PROC MIXED; SAS Institute 1999). For 2003, data collected in the CRD split-plot study, ANOVAs within sample periods included the main effects of EFNs and ant exclusion and the interactive effects on *G. molesta* densities and percentage parasitism of *G. molesta* (PROC MIXED; SAS Institute 1999). Percentage parasitism data were arcsine ($\sqrt{}$) transformed before ANOVA. When ANOVA indicated significant treatment effects, means were separated by the least-squares difference procedure using the Bonferroni adjustment to correct for multiple comparisons (LSMEANS/ADJUST = BON, α = 0.05; SAS Institute 1999). In addition, *G. molesta* shoot infestation data and parasitoid abundance data (from sticky traps) were combined, and correlation analysis was performed by treatment for each sample period of 2003 (29 May, 26 June, 22 July, and 14 August; Spearman's rank correlation; SAS Institute 1999).

Fruit Damage by *G. molesta*. Fruit damage by *G. molesta* was compared for trees with and without leaf EFNs in 2005, the first year that the trees produced substantial amounts of fruit. The study used only two of the four original field replicates (Kearneysville, WV site), as trees at the MD site were destroyed in 2004. To avoid potential differences in fruit load or host plant quality, sampling was confined to trees that did not receive the ant exclusion treatment in previous studies. Five trees per treatment plot (EFNs present, EFNs absent) were randomly selected for sampling. To estimate ant abundance in the canopy, two randomly selected terminals per tree were sampled by limb jarring (16 June 2005). On 28 June (2005), peaches were harvested by circling each tree once and picking 15 of the fruits at random. The fruits were examined visually for external insect injury, cut into quarters, and examined internally for larvae. Each larva was microscopically examined and identified. The percentage of fruits infested with *G. molesta* was averaged over the five sample trees per treatment plot. Separate ANOVAs were performed for percentage fruits injured by *G. molesta* (following arcsine [$\sqrt{}$] transformation) and for ant abundance data (PROC MIXED; SAS Institute 1999).

Specimens of *G. molesta* and Hymenoptera collected in all studies were deposited in a reference collection maintained at the USDA Appalachian Fruit Research Station (Kearneysville, WV).

Results

Parasitic Hymenoptera Abundance. The Chalcidoidea were the dominant parasitic Hymenoptera in 2003. They accounted for >52% of the parasitic wasps collected on sticky traps of trees in both EFN treatments (Fig. 1). Ichneumonoidea comprised 30% of parasitoids collected from trees with EFNs but only 10% of the parasitoids from trees without EFNs. *Trichogramma* sp. accounted for $\approx$5% of the parasitoids collected from both types of trees. Platygastroidea, Proctotrupoidea, and Ceraphronoidea were also represented in the collections of 2003 (Fig. 1). Aphids were not present on trees of either leaf type (with or without EFNs).

A consistent trend of greater parasitic Hymenoptera abundance (species combined) on trees with EFNs than trees without EFNs was apparent in both 2002 and 2003 (Fig. 2). EFNs significantly affected the abundance of parasitic Hymenoptera collected in May 2003 and in June of both years (all dates: ndf = 1, ddf = 3; 18 June 2002: F = 100.6, P = 0.002; 29 May 2003: F = 9.7, P = 0.02; 10 June 2003: F = 4.89, P = 0.04). Significantly more parasitoids were trapped on trees with EFNs than trees without EFNs in May and June
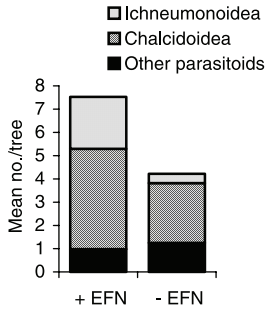
Fig. 1. Parasitic Hymenoptera associated with 'Lovell' peach trees with and without leaf extrafloral nectaries (±EFN). Average adult abundance based on 24-h sticky trap catches summed over seven sample periods in 2003. Other parasitoids were Platygastroidea, Proctotrupoidea, and Ceraphronoidea.

Fig. 3. Interactive effect of ant exclusion treatment and leaf extrafloral nectary presence (+EFN) or absence (−EFN) on *G. molesta* larvae infesting terminal shoots of 'Lovell' peach trees, 29 May 2003. Least-squares means (±SEM) are shown.

of each year (least significant difference [LSD], $P < 0.05$; Fig. 2a and b). Ant exclusion did not significantly affect parasitoid (species combined) abundance. Separate analyses for the relative abundance of Braconidae and *Trichogramma* sp. indicated that they were not significantly affected by EFNs or ants in any sample period.

Grapholita molesta **Abundance and Natural Parasitism Rates.** A significant interactive effect of the EFNs and the ant exclusion treatment was detected for *G. molesta* larval abundance in shoots during the first sample period of 2003 (29 May: ndf = 1, ddf = 6, $F = 65.2, P = 0.02$). When ants were not excluded from the tree canopies, trees with EFNs had significantly fewer flagged shoots than trees without EFNs (LSD, $P < 0.05$; Fig. 3). When ants were excluded, *G. molesta* injury did not differ between trees with or without the EFNs. The EFNs did not significantly affect the pest larval abundance in terminal shoots during the June–August sample periods of 2002 or 2003. No ants were detected on the trees that received ant exclusion treatment in 2003, regardless of EFN phenotype. *Formica nitidiventris* Emery and *Lasius neoniger* Emery were present on control trees of both EFN phenotypes, but
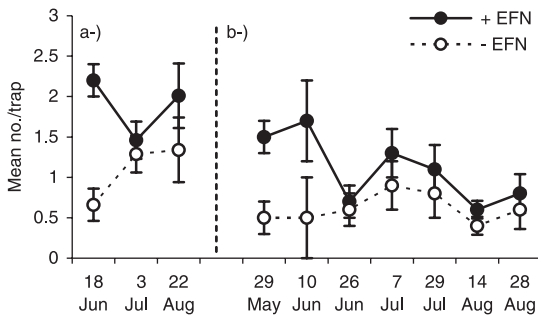
ants were collected more frequently from the trees with EFNs than the trees without EFNs (mean no. ants ± SD: 29 May +EFN = 2.3.0 ± 0.0, −EFN = 0.1 ± 0.3; 26 June +EFN = 2.4 ± 2.9, −EFN = 0.0 ± 0.0; 22 July +EFN = 0.6 ± 0.9, −EFN = 0.0 ± 0.0; 13 August +EFN = 5.1 ± 4.6, −EFN = 0.0 ± 0.0). Aphids were not present on trees of either leaf type (with or without EFNs).

The relative abundance of larval *G. molesta* was highest on trees without EFNs in May 2003 and gradually declined (Fig. 4). Braconids were positively correlated with *G. molesta* larval abundance on trees with EFNs during June (Spearman's $\rho = 0.59, P = 0.02$) but not on trees without EFNs (Fig. 4). The EFNs significantly affected *G. molesta* parasitism by *M. delicatus* (Hymenoptera: Braconidae) in July 2003 (ndf = 1, ddf = 3, $F = 6.8, P = 0.04$; Fig. 5). Percentage parasitism was significantly greater in *G. molesta* larvae on trees with EFNs than trees without EFNs (LSD, $P < 0.05$; Fig. 5).

Fruit Damage by *G. molesta*. EFNs significantly affected ant densities on trees (ndf = 1, ddf = 2, $F = 20.25, P = 0.04$) and fruit injury by *G. molesta* (ndf =

Fig. 2. Effect of 'Lovell' extrafloral nectaries (±EFN) on parasitic Hymenoptera relative abundance based on 24-h sticky trap catches during three sample periods of 2002 (a) and seven sample periods of 2003 (b). Parasitoid abundance data from both trees with and without ant exclusion bands were combined. Geometric means are plotted with 95% CI.
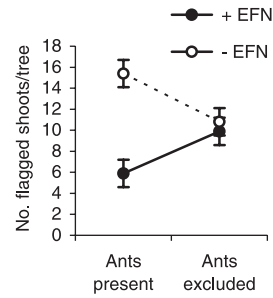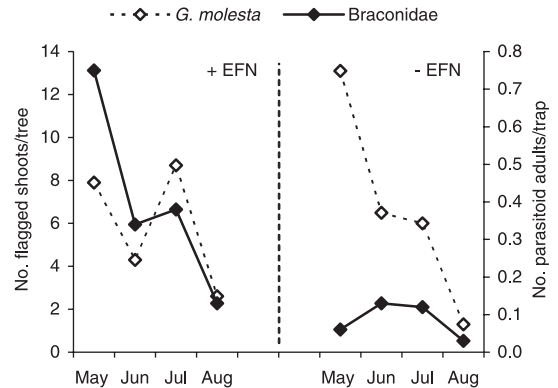

Fig. 4. Average monthly abundances of larval *G. molesta* (Y1 axis), based on visual inspection, and adult Braconidae (Y2 axis), based on sticky trap catches, in plots of 'Lovell' peach trees with leaf extrafloral nectaries present (+EFN) or absent (−EFN), 2003.
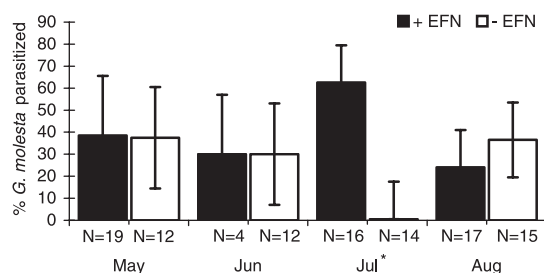
Fig. 5. Monthly rates of *G. molesta* parasitism by *M. delicatus* on 'Lovell' peach trees with leaf extrafloral nectaries present (+EFN) or absent (−EFN), 2003. The number of shoots per sample (*N*) is shown on the X axis, and back-transformed means are plotted with 95% CI. *Significant EFN effect within month detected by ANOVA.

1, ddf = 1, *F* = 361.0, *P* = 0.03) in 2005. Average ant abundance in trees with EFNs was significantly higher than in trees without EFNs (LSD, *P* < 0.05; Fig. 6). The percentage of fruit with *G. molesta* injury was ≈20 times greater on trees lacking EFNs and ants (LSD, *P* < 0.05; Fig. 6).

Discussion

These studies clearly showed that leaf EFNs may enhance naturally occurring biological control of the oriental fruit moth and reduce its damage to peach trees. A significant (greater than two-fold) increase in parasitic Hymenoptera was detected for trees with EFNs in May and June (Fig. 2). Availability of sugar resources such as provided by extrafloral nectar in the spring is particularly important for adult parasitic wasps that rely exclusively on nectar resources (Leius 1960, Quicke 1997). Although an increase in *G. molesta* parasitism was not detected during these months, this significant numerical response to EFNs could have positive implications for biological control later in the season through a variety of mechanisms. Sugar feeding increased the longevity of *M. ancylivorus*, a predominant parasitoid of *G. molesta* in the mid-Atlantic region (Stearns 1928). Sugar resources also can enhance wasp fecundity and attack rates (Powell 1986, Vinson and Barbosa 1987, Olson et al. 2000) and lead to in-

creased time spent searching for hosts (Lewis et al. 1998). We found that *G. molesta* parasitism by the braconid *M. delicatus* increased dramatically on peach trees with EFNs in July 2003 (Fig. 5) when the pest's larvae infest peach fruits in the mid-Atlantic region (Hogmire 1995). The parasitoid's action on the July infestation (fourth or fifth generation) may be especially important in reducing economic damage to the fruits.

The ant exclusion studies revealed that ants associated with the EFNs did not repel the braconid parasitoids nor disrupt their effectiveness against *G. molesta*. In fact, the significant reduction of *G. molesta* on trees with EFNs and ants (no exclusion treatment) in late May (2003) suggests that the ants contributed to a reduction of *G. molesta* during its first two generations (Fig. 3). The ants could have removed or eaten the *G. molesta* eggs or the exposed larvae before they entered the shoots. Tilman (1978) observed that *Formica obscuripes* (Forel) associated with EFNs of *Prunus serotina* (Ehrh.) would remove *Malacosoma americanum* (Fabricius). Way and Cammell (1989) reported that ant removal of eggs of the coconut caterpillar (*Opisina arenosella* Walker) significantly reduced the pest's abundance. The Chinese have relied on ants to suppress fruit injury in citrus orchards for centuries, and anecdotal evidence suggests that fruit production is not possible in some regions of China without the protective actions of ants (Groff and Howard 1925, Olkowski and Zhang 1998). The ≈90% reduction in *G. molesta* damage to fruit on trees with both EFNs and ants (2005) shows that when EFNs are present, naturally occurring biological control agents can contribute significantly in suppressing *G. molesta* when insecticide is not used (Fig. 6).

More research is needed to determine the specific contributions of ants and braconids in the presence and absence of peach EFNs and to explain precise effects (nutritional, attractive, chemical, etc.) of the EFNs on the natural enemies. Moreover, plant breeders and entomologists need to cooperate in reevaluating the wisdom of breeding efforts that discard EFNs from modern peach cultivars. Elimination of the EFNs may have a disastrous effect on natural enemies. Use of natural enemies in peach pest management programs is especially important now that the availability of effective insecticides is diminishing because of increasing problems of insect resistance and regulatory action (Pree et al. 1998, Shearer and Atanassov 2004).
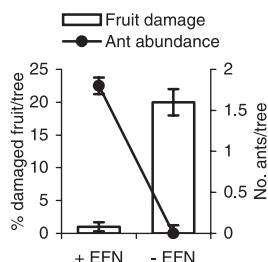
Fig. 6. Effect of leaf extrafloral nectaries (±EFN) on percentage of 'Lovell' fruit (15/tree) infested with *G. molesta* larvae (Y1 axis) and number of ants foraging in tree canopy (Y2 axis), June 2005. Back-transformed means are plotted with 95% CI.

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